Dingoes dining with death

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ABSTRACT

Dingoes (*Canis dingo*) are known for hunting and killing animals to meet their energetic requirements, but like almost all predators they also scavenge animal remains. To improve our understanding of dingo scavenging ecology, we investigated the role of abiotic and biotic factors in shaping carcass utilisation by dingoes and further determined whether dingo scavenging influenced carcass persistence in the landscape. To do so, we monitored visitation and scavenging by dingoes using remote cameras positioned on 119 kangaroo carcasses in open and closed canopy habitats and in warm and cool seasons. The carcasses were monitored across multiple study sites, which incorporated forest, alpine and desert ecoregions in Australia. We found that season played an important role in shaping carcass utilisation by dingoes, as well as carcass persistence. Warmer seasons increased the rate of carcass discovery 6.3-fold in the Forest study site and 4.8-fold in the Alpine study site, and also increased the time dingoes spent feeding on carcasses in the Alpine study site. Further, across all study sites, carcasses persisted at least 4.7 times longer in cool compared with warm seasons. On the other hand, carcass utilisation by dingoes was not influenced by habitat, although carcasses were more likely to persist in open compared with closed canopy habitats in the Alpine study site. Finally, our study showed that dingo scavenging may contribute to substantial carcass removal in certain contexts. Indeed, decreased carcass persistence in the Forest study site was evident in the cool season, when dingo scavenging occurred during the first two weeks of monitoring. The variability in results highlights the complexity of patterns in dingo scavenging and, more broadly, of vertebrate scavenging. It emphasises the need to consider multiple abiotic and biotic factors to properly understand the functional roles of different scavenger species. Longer-term studies with additional seasonal replicates may also yield a more detailed picture of the role of dingoes as apex scavengers.

Key words: Dingo, carcass, carrion, apex scavenger, abiotic and biotic factors

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Introduction

The diet of the dingo (*Canis dingo*), including hybrids (*Canis dingo* x *Canis familiaris*) is well-studied across a range of Australian environments (Doherty *et al.* 2019). There is substantial variability in the prey species dingoes consume and their dietary habits are often linked to the abundance of prey (Corbett and Newsome 1987). Dingoes typically show preferences for medium to large prey, in particular for macropods (e.g. kangaroos) and rabbits (*Oryctolagus cuniculus*; Whitehouse 1977), although rodents and reptiles can also comprise major dietary components (Paltridge 2002). Across resource-poor landscapes, arthropods, fruits and vegetation often supplement their feeding (Spencer *et al.* 2014), and in human-modified environments, livestock and garbage may feature (Brook and Kutt 2011; Newsome *et al.* 2014). Further, while dingoes are well known for hunting and killing animals to meet their energetic requirements, they also scavenge animal remains (Brook and Kutt 2011; Davis *et al.* 2015; Newsome *et al.* 1983).

In Australia, animal carcasses are abundant. In addition to natural deaths of macropods and other herbivores, millions of carcasses are produced from road-kills or as a result of conservation and agricultural culls (Englefield *et al.* 2018). In recent times, Australia has witnessed the production of high densities of animal carcasses in localised areas following mass animal mortality events, or "die-offs", which have occurred as a result of heatwaves, droughts, floods, and bushfires. These carcasses may be utilised by dingoes and could provide an important resource when alternative foods are scarce. Indeed, patterns of dingo scavenging may be linked to fluctuations in their preferred prey (Thomson 1992) and, during drought periods, dingoes have been observed feeding on cattle carcasses, and even cannibalising remains of their own (Allen 2010). Carcasses produced via anthropogenic practices such as hunting and fishing may also provide an important subsidy for dingoes. Dingoes have been recorded scavenging on carcasses of shot deer (Forsyth *et al.* 2014) and the remains of sea-life left behind by recreational fishers (Déaux *et al.* 2018).

Apart from the potential benefits of carcass resources to the dingoes themselves, dingo scavenging may accelerate the break-down of carcasses. Dingoes are the largest native terrestrial mammalian carnivore in Australia, and can form packs of more than 10 individuals, making them capable of quickly consuming large prey items (Thomson 1992). The ability of dingoes to rapidly consume carcasses is important, as carcasses

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may attract and support invasive species (Abernethy *et al.* 2016) or become a hub for disease spread (Jennelle *et al.* 2009). Dingo scavenging may also regulate carcass use by smaller scavengers, either by facilitating access to carcass meat by piercing tough animal hides or by provoking behavioural avoidance through fear effects (Cunningham *et al.* 2018; Wikenros *et al.* 2014). Evidence for dingoes exerting strong suppressive effects on other species via predation is accumulating (e.g. Glen *et al.* 2007; Letnic and Koch 2010; Ritchie *et al.* 2013), but little attention has been paid to understanding the role of dingoes as apex scavengers. This gap in our understanding influences how we think about dingo interactions with other species, including how they influence prey populations, and how they impact the agricultural industry via predation of livestock. It also affects the ecological value that we place on dingoes; for example, as a contributor to important ecosystem services such as carcass removal.

To improve our understanding of dingo scavenging ecology, it is important to explore the basic abiotic and biotic factors that may influence their use of carcasses. It is well established that temperature affects carcass persistence, with warmer conditions promoting microbial and insect activity, which increases carcass decomposition (Payne 1965; Putman 1978). Carcasses in warmer seasons may also provide stronger olfactory attractants (DeVault and Rhodes 2002). Habitat complexity can further affect carcass detection and rates of scavenging, by changing the visual conspicuousness of carcasses. Carcass detection by vertebrate scavengers at the Savannah River site in South Carolina, USA, for example, was highest in open, clear-cut habitats (Turner *et al.* 2017). Similarly, in Poland most vertebrates, including free-roaming domesticated dogs, scavenged on ungulate carcasses more in open grassland compared to closed canopy habitats (Selva *et al.* 2005).

Here we investigate the scavenging patterns of dingoes on hunter-shot kangaroo carcasses at three study sites—an alpine, a forest, and a desert ecoregion—in Australia. Within these study sites we explore the effects of abiotic and biotic factors, including season and habitat, on carcass use by dingoes. To do so, we distributed kangaroo carcasses in warm and cool seasons and across open (i.e. no canopy cover) and closed canopy (i.e. woodland/dune valley) habitats and measured dingo carcass detection rates and scavenging times, as well as rates of carcass persistence. Across all study sites, we predicted that season and habitat would influence carcass use by dingoes. Specifically, we predicted that dingoes would show (1) increased carcass discovery in warmer seasons and in open habitats, and (2) greater foraging activity in cool seasons when competition with insects and microbes is reduced. We also predicted that (3) carcass persistence would be shorter in warmer seasons and as a result of dingo scavenging.

Methods

Study sites

Our study sites cover two locations in New South Wales and one in Queensland, Australia. These sites were selected as they are home to a moderate-sized population of dingoes and represent diverse habitats. In particular, research was undertaken in the Wolgan Valley in the Blue Mountains, eastern New South Wales (NSW) ("Forest" study site; between August 2017 – February 2018), on the Snowy and Botherum Plains in Kosciuszko National Park, southern NSW ("Alpine" study site; between March 2018 – January 2019) and at Ethabuka Reserve in the Simpson Desert, western Queensland ("Desert" study site; between June – November 2018; Figure 1).

The Forest study site is approximately 50 km^2 in size (altitude: 540–680 m) and is positioned on the edge of the Greater Blue Mountains National Park. This area contains a mix of open woodland and grassland habitats, with various *Eucalyptus* species (e.g. *Eucalyptus viminalis* and *E. haemastoma*) and a mix of native (e.g. *Austrodanthonia* sp. and *Themeda triandra*) and introduced (e.g. *Microlaena stipoides*) grasses. The climate is temperate, with average maximum temperatures of 27°C recorded in January and 11°C in July (nearest station 30 km away at Lithgow, records from 1878 - 2020; Bureau of Meteorology 2020).

The Alpine study site encompasses approximately 70 km^2 in the eastern section of Kosciuszko National Park (altitude: 1305–1540 m). This area contains sub-alpine and montane forests and open grasslands. The dominant vegetation in the open grasslands is snow grass (*Poa* sp.), with non-native grass species including *Anthoxanthum odoratum* also abundant. Snow gums (*Eucalyptus pauciflora*) were the most common tree species observed in the closed canopy habitat. The average maximum temperature ranges from 23°C in January to –6°C in July (nearest station 20 km away at Perisher Valley, records from 2010 - 2020; Bureau of Meteorology 2020).

The Desert study site is located on the edge of the Simpson Desert and is a conservation property managed by Bush Heritage Australia. This area is approximately 80 km^2, at elevations between 65 and 120 m. The Simpson Desert is a hot desert, characterised by long, parallel sand dunes (Purdie 1984) and the prevailing habitat is hummock grassland dominated by hard spinifex (*Triodia basedowii*) (Wardle *et al.* 2015). There are differences in vegetation between the sand dune crests and the inter-dune valleys, with the crests lacking any tree cover and the valleys host to stands of gidgee trees (*Acacia georginae*). The climate is arid, with the hottest month, January, averaging maximums of 40°C and the coolest month, June, averaging maximums of 23°C (nearest station 100 km away at Bedourie, records from 1988 - 2020; Bureau of Meteorology 2020).

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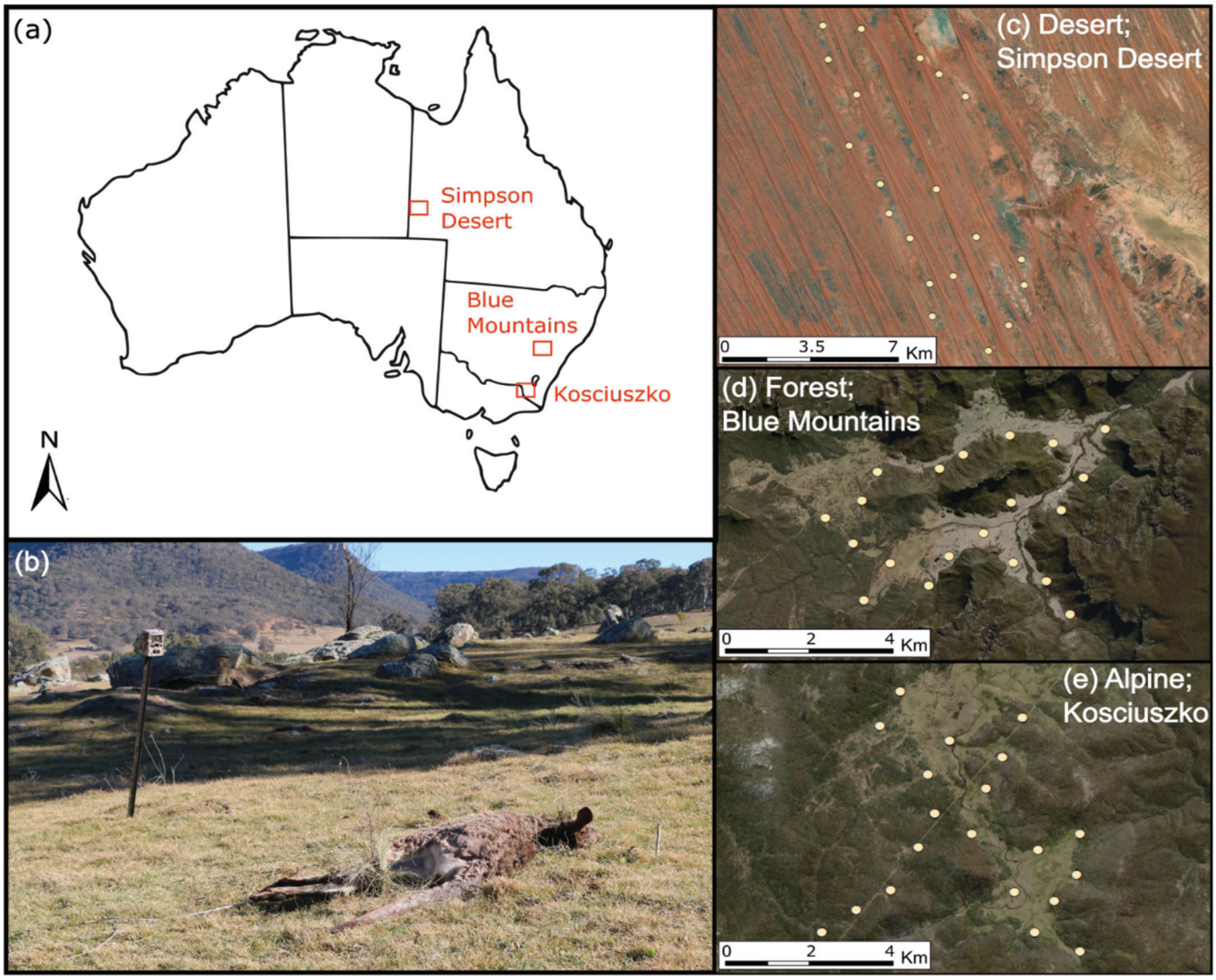

Figure 1. Study area map and carcass site set-up; (a) shows the location of the three study sites in Australia (boxes), (b) provides an example carcass site set-up with the remote monitoring camera positioned ~4 m from the staked kangaroo carcass. Satellite images provide examples of carcass site spatial spread in one study season at (c) the Desert study site, at Ethabuka Reserve in the Simpson Desert, western Queensland, (d) the Forest study site, in the Wolgan Valley, in the Blue Mountains, central NSW, and (e) the Alpine study site, at the Snowy and Botherum Plains in Kosciuszko National Park, south-eastern NSW. Yellow circles on the satellite images mark the position of monitored kangaroo carcasses.

Carcass monitoring

In each study site, we distributed 20 kangaroo carcasses in both cool (winter and autumn) and warm (summer, spring) periods, with half placed in open and half placed in closed canopy habitats. Our study sites included a mix of grassland (open) and woodland (closed) habitats in the Forest and Alpine study sites, and dune crest (open) and valley (closed) habitats in the Desert study site. Open canopy habitats lacked canopy cover and were at least 50 m from any densely forested or vegetated land. Closed canopy habitats had more than 20% canopy cover. We tried to ensure that these closed canopy sites were at least 50 m from any open space; however, this was not possible in the Desert study site due to the general sparsity of trees.

In each season, carcasses were separated by at least 1 km to mitigate scent travel between carcasses. We used dead, adult eastern grey kangaroos (*Macropus giganteus*; Forest and Alpine study sites) or dead adult red kangaroos (*Osphranter rufus;* Desert study site) sourced from nearby management culls. Any carcasses displaying evidence of disease (e.g. heavy parasite loads), were not used. Each carcass was placed into the field without freezing within 24 hours (warm period) or 36 hours (cool period) of collection. Scientific licenses/permits were obtained to relocate the kangaroo carcasses (SL 101901 and SPP WA0006737) and research was approved by the University of Sydney Animal Ethics Committee (Project number: 2017/1173).

To allow for ongoing monitoring and detection of dingoes visiting and feeding on each carcass, we fastened a Reconyx PC800 Hyperfire™ camera trap (Professional Reconyx Inc., Holmen, WI, USA) to a free-standing star picket, approximately 3–4 m away from each carcass. Each camera was programmed to take continuous

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photographs when triggered by thermal movement around the carcass (rapidfire, no wait period). To prevent complete removal of the carcasses from the remote camera monitoring frame, each carcass was secured to the ground by wire attaching the neck and achilles tendon of the animal to two metal stakes spaced ~0.6 m apart. Cameras were used to monitor carcasses until only skin and bones remained (< 4 months); however, at the Alpine study site carcasses were monitored for only 30 days due to the high risk of camera theft.

Data collection

All photographs were tagged according to each new visitation event by one or more dingoes to a carcass, the number of dingoes present, whether the dingoes engaged in scavenging behaviour or not, and the date and time that the observation was recorded. A visitation event was considered new if it occurred ≥ 10 min from the previous visitation event by the same dingo. Different individual dingoes were identified using markings, size and sex. We then extracted four values from the images that we tagged including: "presence", "scavenging", "discovery time" and "total feeding time". Presence was calculated as the number of carcasses that dingoes were recorded visiting, and scavenging was the number of carcasses where they were recorded feeding. Discovery time was calculated in decimal hours as the time between when the carcass was first positioned and the arrival of the first visiting dingo. Total feeding time was calculated as the sum of all feeding events at a given carcass for all dingoes. We calculated the duration of a given feeding event by subtracting the time at the start of the visit from the time at the end of the visit. We rounded all feeding visits to the closest minute; however, for visits less than 30 seconds, we considered the species present for 1 min rather than 0 mins. Using a combination of in-person visual inspection of the carcasses and inspection of camera images, we determined the number of days until complete carcass consumption. A carcass was defined as completely consumed when only skin, hair and/or bone remained.

Statistical analysis

To test each prediction, we ran separate analyses for each study site. This is because our sampling effort differed across study sites (i.e. at the Alpine study site carcasses were monitored for only 30 days, whereas at the Desert and Forest study sites carcasses were monitored until complete decomposition), and because some study sites did not provide enough data points to statistically compare all predictor variables. Before conducting analyses, we also excluded data from one carcass site (from the cool season at the Alpine study site) due to camera theft occurring during the first 3 days of monitoring. We conducted all analyses in R Version 4.0.2 (R Core Team 2020).

To determine whether dingoes showed increased carcass discovery in warmer seasons and in open habitats (*Prediction 1*), we performed survival analyses using Cox proportional hazards models on the time taken for carcasses to be discovered in hours ("survival" package). Survival analyses work well with censored data (Hosmer *et al.* 2008). Carcass discovery data were right-censored because some carcasses were not discovered by dingoes by the end of monitoring periods (i.e. complete carcass decomposition; Forest and Desert study sites, or 1 month post carcass placement; Alpine study site). We ran three separate analyses investigating how long carcass discovery took in each study site. For the Forest (n = 40) and Alpine (n = 39) study sites, season (warm, cool) and habitat (open, closed) were used as the predictor variables. For the Desert study site (n = 40), only habitat (open, closed) was used as a predictor variable, because no dingoes were recorded on the carcasses in the warm period. We tested the proportional hazards assumption by visualising the survival curves and by testing the non-zero slope for the Scholenfeld residuals versus time (Therneau and Grambsch 2000). To visualise the results of these analyses, we separated data into carcasses monitored in warm or cool seasons, and in open and closed canopy habitats and present the Kaplan-Meier estimates of the survival function comparing two survival curves for each study site ("survival", "survminer" and "ggplot2" packages). Finally, we also present the results of log-rank tests, comparing these survival curves.

To test if dingoes showed greater foraging activity in cool seasons (*Prediction 2*), we used generalised linear models (GLMs) to compare foraging activity for dingoes across season (warm, cool) and habitat (open, closed). Foraging data followed a negative binomial distribution and were zero-inflated. This indicated a two-process mechanism for data generation, which we modelled using hurdle models. For the first model, we conducted a GLM with binomial distribution using whether a dingo fed at a carcass as the response variable. For the second model, we conducted a GLM with negative binomial distribution using how long a dingo fed in minutes, from the non-zero data. For the Forest and Alpine study site, season (warm, cool) and habitat (open, closed) were used as the predictor variables in both models, but for the Alpine study site sparse data precluded inclusion of season from the second stage of modelling. For the Desert study site, only habitat was utilised in the models because no dingoes were recorded on the carcasses during the warm period. We visually assessed model predicted values against the residual values to confirm that each model met their necessary assumptions.

To determine whether carcass persistence would be reduced in warmer seasons and as a result of dingo scavenging (*Prediction 3*), we performed further survival analyses using Cox proportional hazards models on data for the time taken in days for complete carcass decomposition. Carcass persistence data were right-censored because some carcasses were not completely decomposed by the end of monitoring periods (i.e. n = 12 carcasses, during the cool monitoring period in the Alpine study site). We ran separate analyses investigating how long carcass decomposition took in each

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study site. To create our models, we used a combination of three predictor variables including season (warm, cool), habitat (open, closed) and presence or absence of dingo scavenging during the first two weeks of monitoring (as a binary measure). For the Forest study site, we also included the interaction term between season and dingo scavenging, to examine whether dingo scavenging influenced carcass persistence across different seasons. We did not have enough data to include this term in the Alpine or Desert study site, as only one carcass was scavenged by dingoes in the cool season at the Alpine study site and no carcasses were scavenged by dingoes during the warm season at the Desert study site. Instead, we conducted a second round of analyses for these two study sites, excluding data from the seasons where dingo scavenging was rare or absent. For these analyses, we used habitat (open, closed) and presence or absence of dingo scavenging during the first two weeks of monitoring (as a binary measure). The presence or absence of dingo scavenging in the first two weeks was used rather than the presence of dingo scavenging across the entire monitoring period, as this is when most carcass biomass was lost. It also enabled us to exclude data where dingoes appeared on mostly-decomposed carcasses to chew on bones and so did not contribute much to the removal of carcass biomass. For all analyses, we tested the proportional hazards assumption, as for analyses conducted for prediction 1. To visualise the results of these analyses, we separated data into carcasses where dingo scavenging was present or absent during the first two weeks of monitoring and where carcasses were monitored in warm or cool seasons, and presented Kaplan-Meier estimates of the survival function comparing up to four survival curves for each study site. Again, we also presented the results of log-rank tests that compare these survival curves. For any significant interactions, we calculated the pairwise comparisons between group levels with Bonferroni corrections for multiple testing.

Results

We conducted successful camera trials on 119 kangaroo carcasses over a total of 9,427 days, collecting and analysing 54,823 images of dingoes, which yielded a total of 540 dingo visitation events (see the photo appendix for further observations and comments on dingo behaviour observed around carcasses during the study).

Prediction 1: Increased carcass discovery in warmer seasons and in open habitats

Across all study sites, a total of 59 (50%) of the 119 carcasses were visited by dingoes, and 42 carcasses (35%) were fed upon by dingoes (Figure 2). The Forest study site had the highest carcass visitation (32 carcasses; 80%) and scavenging rates (25 carcasses; 63%) by dingoes (Figure 2). Dingoes visited 17 (44%) carcasses and scavenged 11 (28%) carcasses in the Alpine study site (Figure 2). In the Desert study site, dingo carcass visitation and scavenging were the lowest of all sites (visitation: 10 carcasses or 25% and scavenging: 6 carcasses or 15%; Figure 2). Dingoes generally discovered carcasses in the first 1 to 6 days, with carcass discovery in the Forest study site occurring between days 1 and 34, in the Alpine study site between days 1 and 24 and in the Desert study site between days 3 and 17. It took dingoes an average (± se) of 197 ± 26 hours to discover carcasses, with average carcass discovery times in the Forest study site: 215 ± 45 hours, the Alpine study site: 158 ± 33 hours, and the Desert study site: 209 ± 36 hours (averages based on only those carcasses that were visited by dingoes; Figure 3).

In the Forest and Alpine study sites, kangaroo carcasses were discovered more quickly by dingoes in the warm season compared to the cool season (Table 1, Figure 4). In the warm season compared to the cool, carcasses were discovered by dingoes approximately 6.3-fold faster in the

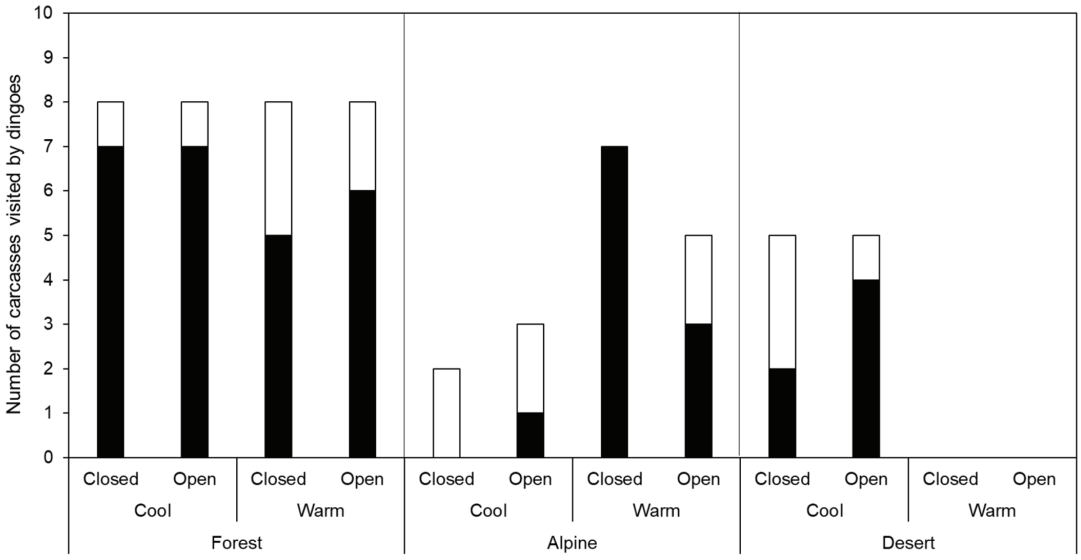

Figure 2. Dingo visitation of kangaroo carcasses (n = 119) across cool and warm seasons, open and closed canopy habitats, and in the Forest, Alpine and Desert study sites. The numbers of carcasses visited by dingoes are separated into the carcasses fed upon by dingoes (black bars) and carcasses visited but not fed upon by dingoes (white bars).

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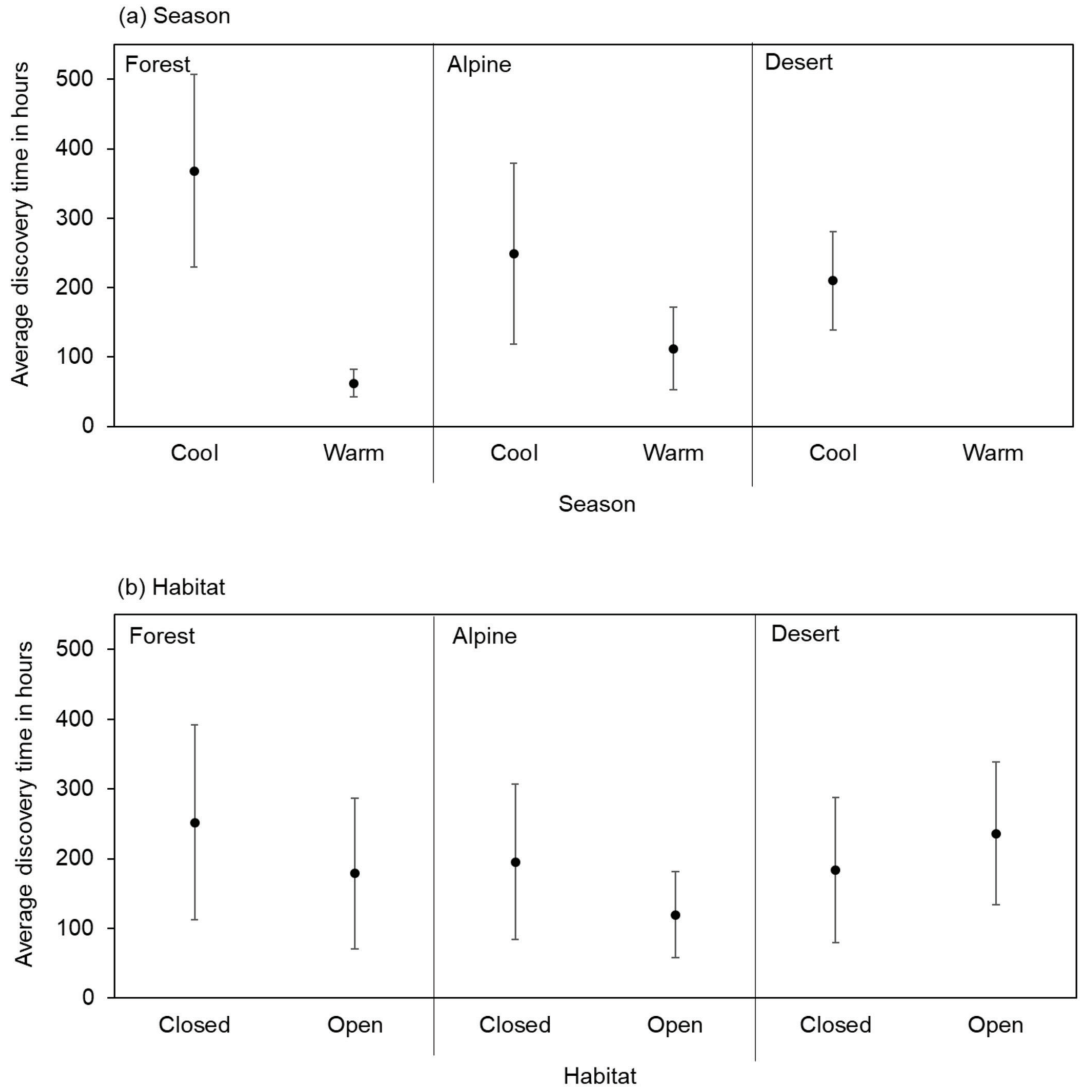

Figure 3. The average time in hours (± 95% confidence intervals) it took for carcasses to be discovered by dingoes during different (a) seasons and (b) habitats, across the Forest (n = 30), Alpine (n = 18) and Desert (n = 10) study sites. Averages and confidence intervals consider only those carcasses that were visited by dingoes. No dingoes visited carcasses in the warm period in the Desert study site.

Forest study site, and 4.8-fold faster in the Alpine study site (Table 1). For the Desert study site, no carcasses were discovered by dingoes in the warm season (Figure 4). Habitat did not influence carcass discovery by dingoes in any study site (Table 1, Figure 4).

Prediction 2: Greater foraging activity in cool seasons

Dingoes generally fed on carcasses when they visited (~71% of visitations). Feeding in the Forest study site occurred until day 52, and in the Alpine and Desert study site until day 17. Of the carcasses that dingoes fed upon, they spent an average (± se) of 61 ± 11 minutes feeding. They fed on carcasses for an average of 52 ± 14 minutes at the Forest study site, 70 ± 21 minutes in the Alpine study site, and 80 ± 28 minutes in the Desert study site.

There were no associations between the presence of feeding, or the amount of time spent feeding, by dingoes on kangaroo carcasses, in warm and cool seasons or in open and closed canopy habitats at the Forest study site (Figure 5, Table 2). In the Alpine study site, dingoes fed on more carcasses in the warm compared to the cool season but there were no differences between the presence of dingo feeding across open and closed canopy habitat types (Figure 5, Table 2). At the Desert study site, dingoes spent longer feeding on carcasses in the closed canopy habitat compared to the open habitat (Figure 5, Table 2).

Prediction 3: Reduced carcass persistence in warm seasons and where dingoes scavenge

Carcasses persisted for an average (± se) of 16 ± 4 days, with complete carcass decomposition taking between 2 and 66 days (Figure 6). In the Forest study site, carcasses persisted for an average (± se) of 19 ± 4 days (range 3 – 66 days; Figure 6). In the Alpine study site, carcasses persisted for an average (± se) of 16 ± 5 days (range 2 – 30 days; keeping in mind that carcass monitoring

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Table 1. Cox proportional Hazards models testing for differences in carcass discovery time in hours across season and habitat in the Forest, Alpine, and Desert study sites, with parameter estimates, Hazard ratios, and associated standard error (SE). No dingoes visited carcasses in the warm period in the Desert study site.

Variables	Estimate	Hazard ratios**	SE	z-value	*p*
Forest study site (n = 40)					
Season	1.842	6.311	0.511	3.61	<0.001*
Habitat	0.698	2.010	0.378	1.85	0.065
Alpine study site (n = 39)					
Season	1.578	4.847	0.518	2.72	0.006*
Habitat	0.552	1.736	0.518	1.07	0.287
Desert study site (n = 40)					
Habitat	-0.240	0.787	0.639	-0.38	0.707

* indicates significance; $p < 0.05$. ** Hazard ratios = exp(Estimate) and estimates the magnitude of the effect. Carcasses monitored in the warm season in the Forest study site, for example, were found 6.3 times faster by dingoes than carcasses monitored in cooler months in the Forest study site.

was capped at 30 days at this study site; Figure 6). In the Desert study site, carcasses persisted for an average (± se) of 14 ± 4 days (range 3 – 49 days; Figure 6).

Across all study sites, kangaroo carcasses persisted at least 4.7-fold longer in the cool seasons compared to warm seasons (Table 3, Figures 7, 8a, 9a). Dingo scavenging during the first two weeks of carcass monitoring reduced carcass persistence by 1.1-fold in the Forest study site (Table 3). At this study site, the interaction between season and dingo scavenging was also significant (Table 3, Figure 7). The post-hoc adjusted pairwise analyses indicated that in the cool period, carcass persistence was lower where dingoes scavenged in the first two weeks, compared to carcasses that were not scavenged by dingoes during this time (Bonferroni adjusted pairwise log rank test: $p = 0.016$). On the other hand, for the warm season, dingo scavenging during the first two weeks of monitoring was not found to influence rates of carcass persistence (Bonferroni adjusted pairwise log rank test: $p = 0.196$). At the Desert and the Alpine study sites, there was no difference in carcass persistence between carcasses where dingo scavenging was present or absent in the first two weeks (Table 3, Figures 8b, 9b). This was the case when all seasons were considered, or when only the warm or the cool season was considered in the Alpine and Desert study sites, respectively (Table 3, Figure 8b, 9b). Finally, in the Alpine study site, carcasses were 4.1-fold more likely to persist in open compared with closed canopy habitats, and there were no differences in carcass persistence times across habitats in the Forest or the Desert study site (Table 3).

Discussion

We present the single largest study examining patterns of dingo scavenging in Australia to date. It has revealed widespread carcass use by dingoes, which foraged at carcasses across nearly every season and habitat studied. It also indicated substantial variation in dingo scavenging across different Australian ecoregions. For example, in the Forest and Alpine study sites dingoes detected carcasses more quickly in the warmer season, but in the Desert study site carcasses were detected by dingoes only in the cool season. Further, foraging activity by dingoes was increased in warmer seasons, but only in the Alpine study site, and closed canopy habitats saw increased foraging activity, but only in the Desert study site. Finally, our study showed that dingo scavenging may contribute to substantial carcass removal in certain contexts. Indeed, decreased carcass persistence in the Forest study site was evident in the cool season, at carcasses where dingo scavenging occurred during the first two weeks of monitoring. We expand upon our findings in relation to our initial predictions and discuss potential management implications of the study.

Prediction 1: Greater carcass discovery in warmer seasons and in open habitats

Carcass discovery by dingoes was primarily influenced by season, with dingoes generally discovering carcasses at a greater rate in warmer seasons in support of prediction 1. Against this prediction, however, open habitats did not increase carcass detection by dingoes at any study site. Rather than relying on visual identification of the carcasses, dingoes probably use decomposition odour to detect carcass resources across the different habitat types. Odour is a dominant stimulus used by mammals to detect carcasses and other food resources (DeVault and Rhodes 2002; Henry 1977) and, while the propagation of odour cues may decrease in complex habitats (Verheggen *et al.* 2017), these cues were probably still strong enough to be detected by dingoes at a distance. Forsyth *et al.* (2014) found that dingoes readily discovered ungulate carcasses in forested habitats, suggesting that dingoes there were relying on odour cues to detect carcasses. Studies with other canid species such as red foxes (*Vulpes vulpes*)

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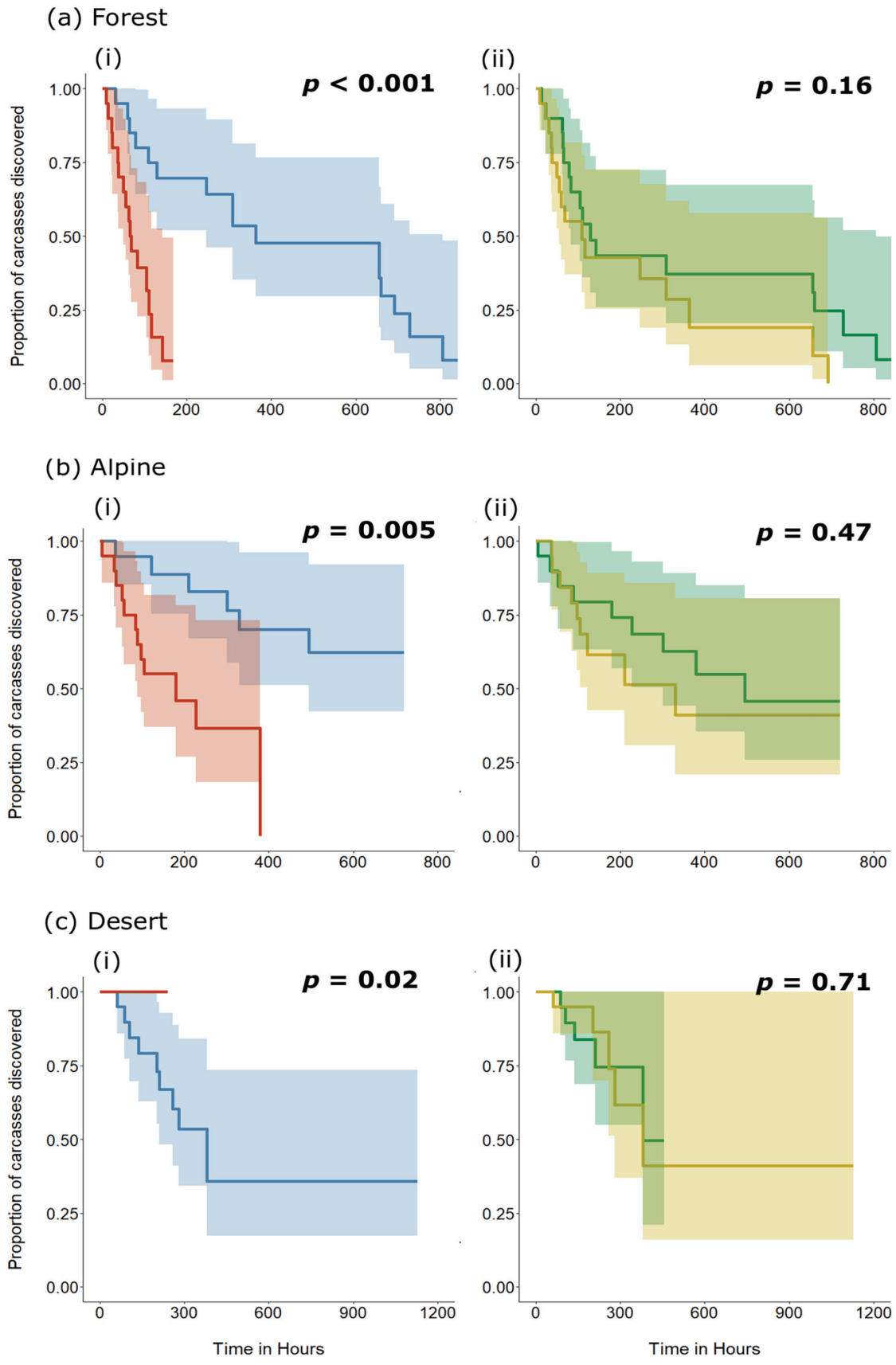

Figure 4. Kaplan-Meir estimate of the survival function for carcass discovery time by dingoes, divided into carcasses at the (a) Forest study site (n = 40), the (b) Alpine study site (n = 39), and the (c) Desert study site (n = 40), where (i) seasons were warm (red) or cool (blue), and where (ii) habitats were open (yellow) or closed (green) canopy. Light shading shows 95% confidence intervals. The p-values are from the log-rank tests comparing the survival curves.

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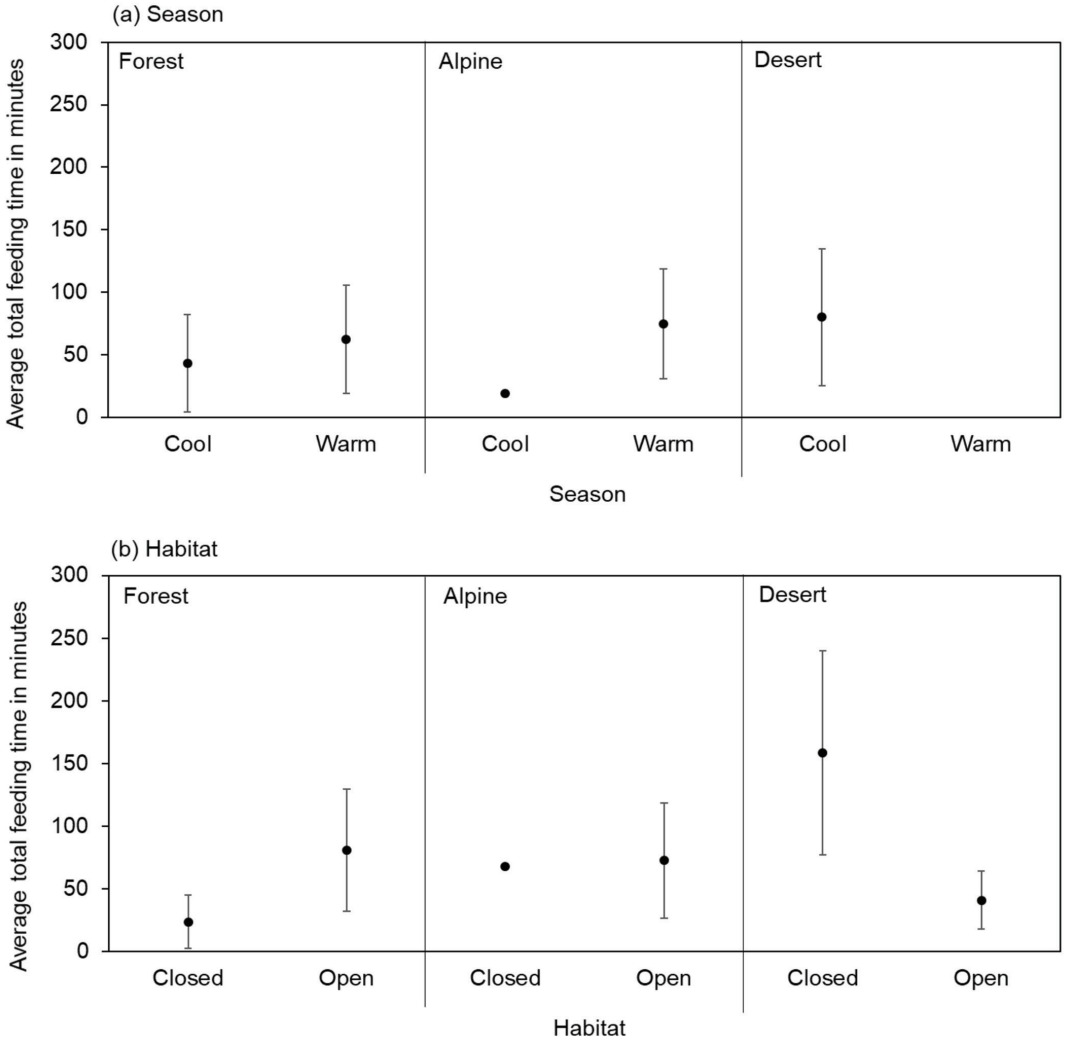

Figure 5. The average time in minutes (± 95% confidence intervals) dingoes fed on carcasses during different (a) seasons and (b) habitats, across Forest (n = 24), Alpine (n = 11), and Desert (n = 6) study sites. Averages and confidence intervals consider only those carcasses that were visited and fed upon by dingoes. No dingoes visited carcasses in the warm period in the Desert study site.

and wolves (*Canis lupus*) have also shown even carcass visitation across open grassland and woodland habitats (Selva *et al.* 2003).

Higher temperatures generally increase microbial activity on carcasses (Payne 1965; Putman 1978), which in turn enhances decomposition odour. Increased odour driven by warmer temperatures probably explains why dingoes showed greater rates of carcass discovery in the Forest and Alpine study sites during the warm season. It is also probable that seasonal differences in carcass discovery were influenced by local dingo densities at the time. Animal density is an important factor influencing scavenging efficiency (Cunningham *et al.* 2018; Huijbers *et al.*; Morales-Reyes *et al.* 2017; Ogada *et al.* 2012). At the Desert study site, low dingo density may explain why we observed no dingo scavenging during the warmer period, against prediction 1. Supporting this idea, 10 camera traps monitoring roads during our study also failed to detect any dingo activity during the warmer study period. In arid regions, animal population densities are typically low, especially compared to those of the more productive temperate regions. This can lead to reduced scavenger diversity and to fewer carcasses being scavenged. In the Sonoran Desert, in the USA, for example, only four scavenging species were recorded, and they scavenged only 40% of bird carcasses monitored (Rogers *et al.* 2014). Similarly, at our Desert study site, there were relatively few individual dingoes observed visiting carcasses (~3 individuals observed on our carcass cameras) and dingoes detected only 25% of carcasses. In contrast, in more productive areas, including the Forest study site, high dingo densities (~14–18 individuals observed on our carcass cameras) explain why so many carcasses were detected by dingoes (80% of carcasses monitored). Dingo numbers are also unlikely to change dramatically across seasons in these more productive areas, explaining why dingoes detected the same number of carcasses between seasons at the Forest study site (16 carcasses during both the warm and cool seasons). Compared to the Desert study site (warm:

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Table 2. Results of the hurdle models, testing for differences in the total time in minutes dingoes spent feeding at the Forest (n = 40), Alpine (n = 39), and Desert (n = 40) study sites. Tables show results of the: (a) generalised linear model (GLM) with binomial distribution testing whether dingoes fed at carcasses, and (b) GLM with negative binomial distribution testing how much time dingoes spent feeding at carcasses that they decided to feed from. No dingoes visited carcasses in the warm period in the Desert study site.

Variables	Estimate	SE	t-value	*p*
(a) Presence of feeding				
Forest study site				
Intercept	0.740	0.582	1.27	0.204
Season	-0.648	0.664	-0.98	0.329
Habitat	0.219	0.662	0.33	0.741
Alpine study site				
Intercept	-2.517	1.057	-2.38	0.017*
Season	3.029	1.150	2.64	0.008*
Habitat	-1.025	0.860	-1.19	0.233
Desert study site				
Intercept	-2.197	0.745	-2.95	0.003*
Habitat	0.811	0.932	0.87	0.384
(b) Time spent feeding				
Forest study site				
Intercept	2.575	0.719	3.58	<0.001*
Season	0.224	0.749	0.30	0.765
Habitat	1.314	0.745	1.76	0.078
Log(theta)	-1.498	0.779	-1.92	0.054
Alpine study site				
Intercept	4.183	0.443	9.44	<0.001*
Habitat	0.066	0.730	0.09	0.928
Log(theta)	-0.302	0.519	-0.58	0.560
Desert study site				
Intercept	5.066	0.269	18.81	<0.001*
Habitat	-1.352	0.337	-4.02	<0.001*
Log(theta)	1.975	0.649	3.05	0.002

* indicates significance; $p < 0.05$.

0 carcasses detected by dingoes, cool: 10 carcasses detected by dingoes), where mammalian predator home ranges are often large (Newsome *et al.* 2017), in temperate forest regions dingoes often have smaller and more stable home ranges, as they need not travel as far in search of food (Harden 1985).

Prediction 2: Greater foraging activity in cool seasons

Dingoes did not increase their foraging activity in cool seasons, against prediction 2. Their rapid discovery of carcasses in the warm season may have enabled them to effectively compete with other scavengers and decomposers including microbes and insects during this time. Further, their tendency to return to carcasses to scavenge bones and dried skin (which decomposed or were consumed by insects more slowly than the carcass flesh) allowed them to continue feeding on carcasses in the warm period even when the majority of carcass biomass had been removed.

Foraging activity by the dingo was likely dependent on the availability of alternative resources in the surrounding environment and by dingo dietary preferences. Previous studies have shown that animals

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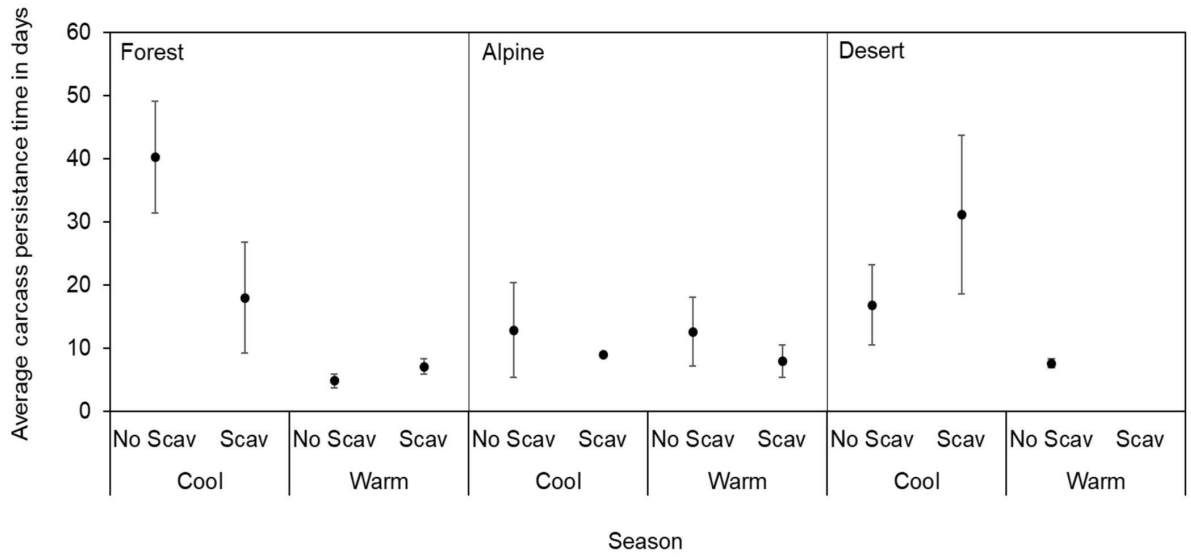

Figure 6. The average time in days (± 95% confidence intervals) that carcasses persisted during different seasons and where dingo scavenging was present (Scav) or absent (No Scav) during the first two weeks of carcass monitoring in the Forest (n = 40), Alpine (n = 28), and Desert (n = 40) study sites. Averages and confidence intervals consider only those carcasses that reached complete decomposition (i.e. 11 carcasses from the cool season in the Alpine study site were excluded from these calculations). No dingoes visited carcasses in the warm period in the Desert study site.

Table 3. Cox proportional Hazards models testing for differences in carcass persistence time across season, habitat and presence or absence of dingo scavenging during the first two weeks of carcass monitoring in the Forest, Alpine, and Desert study sites, with parameter estimates, Hazard ratios, and associated standard error (SE).

Variables	Estimate	Hazard ratios**	SE	z-value	*P*
Forest study site, both seasons (n = 40)					
Season	4.664	106.012	0.857	5.44	<0.001*
Habitat	0.104	4.967	0.360	0.29	0.773
Dingo scavenging	1.603	1.109	0.575	2.79	0.005*
Season × Dingo scavenging	-2.698	0.067	0.752	-3.59	<0.001*
Alpine study site, both seasons (n = 39)					
Season	2.028	7.596	0.650	3.12	0.002*
Habitat	1.421	4.142	0.478	2.98	0.003*
Dingo scavenging	0.895	2.447	0.529	1.69	0.090
Alpine study site, warm season only (n = 20)					
Habitat	2.490	12.060	0.810	3.07	0.002*
Dingo scavenging	0.906	2.475	0.574	1.58	0.115
Desert study site, both seasons (n = 40)					
Season	1.548	4.702	0.472	3.28	0.001*
Habitat	0.069	1.071	0.336	0.21	0.837
Dingo scavenging	-0.952	0.386	0.538	-1.77	0.077
Desert study site, cool season only (n = 20)					
Habitat	-0.347	0.707	0.475	-0.73	0.465
Dingo scavenging	-0.975	0.377	0.547	-1.78	0.075

* indicates significance; $p < 0.05$. ** Hazard ratios = exp(Estimate) and estimates the magnitude of the effect. Carcasses monitored in the cool season in the Forest study site, for example, were 106.0 times more likely to persist for longer than carcasses monitored in warmer months in the Forest study site.

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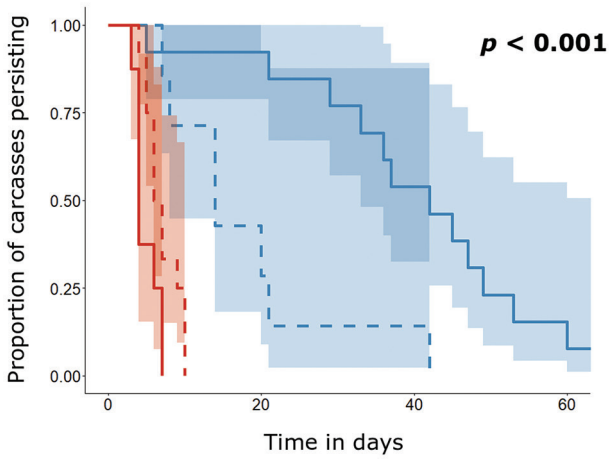

Figure 7. Kaplan-Meir estimate of the survival function for carcass persistence, divided into carcasses at the Forest study site, where seasons were warm (red) or cool (blue), and dingo scavenging was present (dashed line) or absent (solid line). Light shading shows 95% confidence intervals. The p-values are from the log-rank tests comparing the survival curves.

increase their consumption of carcasses during seasons when live prey populations are reduced, such as following winter snows (Olson *et al.* 2016; Selva *et al.* 2005). Similarly, while scavenging by dingoes has been recorded during drought periods, they may consume less carrion biomass when other prey is readily available (Allen 2010; Doherty *et al.* 2019). This is because, despite being opportunists, dingoes still hold preferences for certain prey types, such as macropods (Robertshaw and Harden 1986; Whitehouse 1977), and foraging preferences probably also extend to capturing live prey over scavenging. In the Forest study site, food availability probably was relatively constant over the warm and cool study seasons, explaining why dingoes fed evenly at carcasses across both time periods. Supporting this hypothesis, while we did not conduct counts, we did note highly abundant kangaroo and wallaby populations across both seasons at this study site. In the Alpine study site, on the other hand, lower food availability in the warm season may explain why dingoes increased their foraging activity on carcasses during this time (December 2018). This could have reflected the dynamics of their preferred prey; indeed, kangaroo and wallaby numbers could have been suppressed following the winter snow that fell from April to September. It is also possible that dingoes had access to other carcasses in the cool season. Pig (*Sus scrofa*) and deer (*Cervus* spp.) culls were carried out by the National Parks and Wildlife Service during this time (March 2018) and resulted in the production of carcasses in the study site. Finally, this result might have further been a function of our sampling method. At the Alpine study site, during the cool season, 12 carcasses persisted past the one-month monitoring period. Dingo scavenging may have occurred after we removed the monitoring cameras.

Prediction 3: Reduced carcass persistence in warm seasons and where dingoes scavenge

Season was an important determinant of carcass persistence, with carcass biomass decomposing rapidly in warmer seasons at all study sites. This result supported part of our third prediction that carcasses would persist for shorter times in warmer seasons and can probably be attributed to increased insect and microbial activity on carcasses as a result of warmer temperatures (Putman, 1978). Also supporting our third prediction, in the Forest study site, we found a relationship between the presence of dingo scavenging and a decreased probability of carcass persistence. Reduced carcass persistence has been associated with the presence of obligate scavengers such as turkey vultures (*Cathartes aura*) and black vultures (*Coragyps atratus*; Hill *et al.* 2018), but also with top carnivores, such as the Tasmanian devil (*Sarcophilus harrisii*; Cunningham *et al.* 2018). Our results suggest that like these animals, dingoes could play an important role in carrion removal, although their role is likely to vary according to other factors, such as season. Indeed, in the Forest study site dingo scavenging reduced carcass persistence only during the cool season. Similarly, no effect of dingo scavenging was found during the warm season in the Alpine study site, even though dingoes fed frequently on the kangaroo carcasses. These findings were unsurprising, as vertebrates often play a greater role in carcass removal when temperatures are cooler and competition with insects and microbes is reduced (DeVault *et al.*, 2003). In the Desert study site, on the other hand, scavenging did not influence carcass persistence in the cool season. Variation in the foraging efficiencies of individual dingoes could explain these location-based differences. Dingoes in the Desert study site, for example, often spent substantial time chewing bones to remove the tails from kangaroo carcasses. In the Forest study site, on the other hand, there were several cases where dingoes primarily targeted the stomach area and rump meat, which led to faster biomass loss compared to when they spent time chewing on bones.

It is also important to consider that our results on the effects of dingo scavenging on carcass persistence may have represented a correlative effect. Indeed, we did not consider the impacts of scavenging by other species at any of our study sites. Aside from the impacts of insects and microbes, especially in the warmer seasons, carcass persistence would have likely been affected by smaller scavenging species, along with other dominant scavengers. These animals may have avoided feeding on carcasses visited frequently by dingoes (i.e. due to fear effects). Conversely, dingo scavenging could also facilitate feeding by these animals. Smaller scavengers may associate with larger species that inadvertently provide food (Stahler *et al.* 2002), and scavenging communities frequently show nested patterns on carcasses where highly efficient scavengers are present

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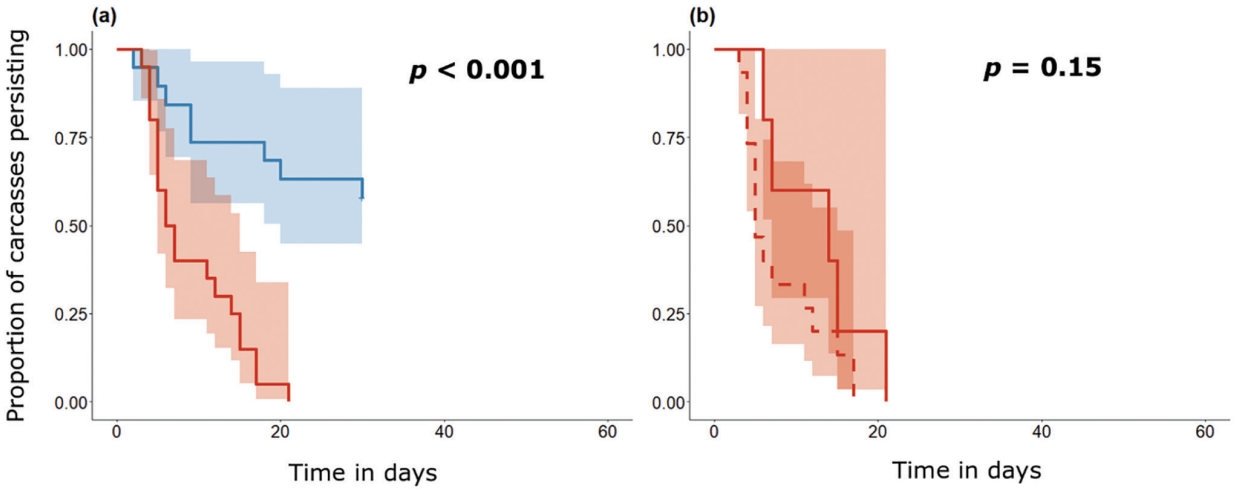

Figure 8. Kaplan-Meir estimate of the survival function for carcass persistence, divided into carcasses at the Alpine study site, across (a) warm (red) or cool (blue) seasons, and (b) in the warm season only, when dingo scavenging was present (dashed line) or absent (solid line). Light shading shows 95% confidence intervals. The *p*-values are from the log-rank tests comparing the survival curves.

(Sebastián-González *et al.* 2016). In the Alpine study site, another dominant scavenger, the feral pig, was also recorded frequently on carcasses and in the Forest and Desert study site, red foxes and wedge-tailed eagles (*Aquila audax*) too were recorded frequently. Future studies should therefore focus on teasing out the relative effects of dingoes and other major scavengers on carcass persistence.

Study implications and future research

Several important points emerge from our study that could be useful in future research on dingo scavenging ecology. First, in agreement with previous studies on vertebrate scavenging and carcass persistence (e.g. Forsyth *et al.* 2014; Selva *et al.* 2005; Turner *et al.* 2017), seasonal effects have been revealed as important in contributing to patterns in dingo scavenging and carcass decomposition. Seasonal changes in carrion utilisation, presumably driven by temperature but also by scavenger population densities, may not only affect how quickly dingoes detect carcasses, but also whether any carcasses are detected by dingoes in the first place and the effects they have on carcass removal. This could be an important consideration in certain regions, such as deserts, where lower animal densities may reduce carcass detection and therefore use. Similarly, prey availability may also differ across seasons, and this could influence how much dingoes feed on carcasses. Thus, surveying prey populations (e.g. macropods and rabbits) during different seasons would benefit future studies. Second, while some factors such as habitat might not always appear important to dingo scavenging or carcass persistence, the effects they have

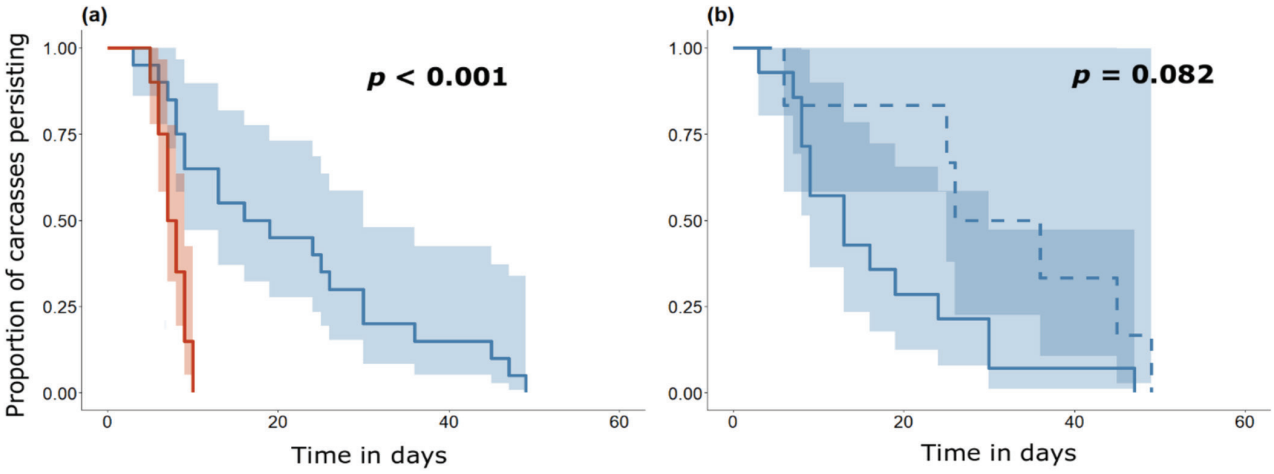

Figure 9. Kaplan-Meir estimate of the survival function for carcass persistence, divided into carcasses at the Desert study site, across (a) warm (red) or cool (blue) seasons, and (b) in the cool season only, when dingo scavenging was present (dashed line) or absent (solid line). Light shading shows 95% confidence intervals. The p-values are from the log-rank tests comparing the survival curves.

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will likely differ with study location, and habitat factors should still be considered in future studies. Third, while not as important as season in determining how long carcasses persist, dingo scavenging may help to accelerate carcass decomposition. Fully teasing out the role of dingoes in accelerating decomposition, however, will depend on simultaneous analysis of dingo and insect use of carcasses, as well as carcass use by other vertebrate scavenger species. Longer term studies with additional seasonal replicates will also yield a more detailed picture of the role of dingoes as apex scavengers.

Finally, it is important to consider that we conducted our study during periods when food resources were readily available. During drought, dingoes may rely on carcasses far more than we observed. Similarly, other weather extremes such as high rainfall events or wildfire might change how they interact with carcasses; for example, by either reducing their use of carcasses as alternative prey resources increase or decrease, or by increasing or decreasing their use as dingo densities and/or competition change. We therefore suggest that, along with incorporating habitat and seasonal factors, surveying prey populations and conducting longer-term studies, future work should consider how dingo scavenging changes across periods of high and low productivity. Further studies should also consider whether regular carcass production (i.e. especially via anthropogenic practices such as culling) influences dingo scavenging and, following this, the number or activity of dingoes in an environment. Understanding whether anthropogenically produced carcasses sustain dingoes through droughts, and whether they focus dingo activity or increase dingo populations in certain areas, will ultimately lead to better-informed land management strategies.

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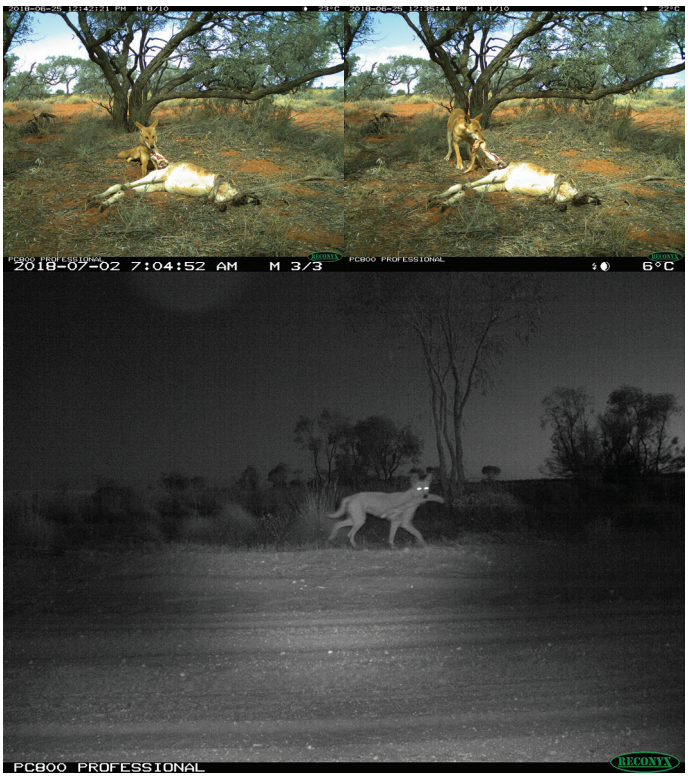
APPENDIX 1

A1. In most cases, dingoes visited carcasses alone or in pairs. Occasionally, however, dingoes were observed around carcasses in large numbers. This image shows a dingo pack investigating a kangaroo carcass at the Forest study site, in the Wolgan Valley, NSW. Ten individuals are pictured here but using sequential pictures we were able to determine that at least 13 individuals were present in the surrounding area.



A2. Dingoes often fed preferentially on kangaroo tails (top images). This preferential feeding behaviour was most prominent at the Desert site in the Simpson Desert, QLD, where dingoes sometimes removed the tail for a 'take-away meal' (bottom image).

A3. Dingo scavenging may lead to rapid removal of carcass biomass. This image shows two dingoes, which consumed this 30 kg kangaroo carcass over three days in the Alpine study site, in Kosciuszko National Park, NSW.

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APPENDIX I

A4. Carcasses are used as a source of sustenance by dingoes, but they may also be a social point of interest. This image shows a female dingo scent marking around a kangaroo carcass at the Desert site, in the Simpson Desert, QLD.

A5. Apart from scent marking, dingoes were also occasionally recorded rolling in the grass or sand surrounding carcasses. This image shows a dingo rolling in a kangaroo carcass at the Forest study site, in the Wolgan Valley, NSW.

A6. Dingoes were commonly observed howling at carcass sites. Occasionally, after howling, additional dingoes would appear at the carcass site to scavenge. These images show a dingo howling at a carcass site at the Alpine study site in Kosciuszko National Park, NSW.

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APPENDIX 1

A7. Dingoes were rarely observed at carcass sites when other species were present. In this image, a dingo pup is pictured at a kangaroo carcass with an Australian raven (*Corvus coronoides*), at the Forest study site, in the Wolgan Valley, NSW.

A8. Dingoes are apex predators, but they often showed vigilance behaviour when visiting carcasses. Some of this behaviour may have occurred due to detection of the wildlife camera, but they may also be responding to the presence of other dingoes, humans and other large animals that may be present at the study sites (e.g. feral pigs). This image shows two dingoes displaying vigilance behaviour around a kangaroo carcass at the Alpine study site, in Kosciuszko National Park, NSW.

A9. Dingoes may interact with insect scavengers at carcass sites. In these images, a dingo displays behaviours indicative of disturbance or interference by swarming European wasps (i.e. snapping at wasps around its head) at the Alpine study site in Kosciuszko National Park, NSW.

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